

Cod (*Gadus morhua* L.) migration speeds and transport relative to currents on the north-east Newfoundland Shelf

G. A. Rose, B. deYoung, and E. B. Colbourne

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Cod were tracked during shoreward migrations across the north-east Newfoundland shelf for 13, 9, and 36 d in the spring of 1990, 1991, and 1992, respectively, with echo-sounder-equipped vessels. Mean daily ground speeds ranged from 0.08–0.28 m s⁻¹ in the three years (max. 0.68 m s⁻¹) over distances up to 59 km (mean daily displacements from 1990–1993 were 10, 24, and 7 km). Mean migration headings were identical in the three years (198°). Cross-track error was smaller and fish were older in 1990 than in 1991 or 1992. Movements along the migration route (198°) coincided with fish movements off the bottom and increasing sea temperatures (325 m station, rises in 2°C isotherm). In 1992, swimming speeds assessed by subtracting currents from ground speeds averaged 0.10 m s⁻¹ (0.23 bl) (maximum 0.28 m s⁻¹; 0.64 bl s⁻¹). After spawning abated, cod exhibited directed movements shoreward. By comparing ground and swimming speeds, we examined hypotheses on passive and active transport. At times, cod actively migrated with advancing flows (ground speeds > swimming speeds), and tended to stem retreating flows (but not always). In contrast, the strong flows across the route (90° to the mean direction) had little effect on cod movements.

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Introduction

The migratory life cycles of fishes can be considered to be adaptations towards abundance, especially in the high latitudes (Nikolskii, 1963; Harden Jones, 1968; Northcote, 1978). In simple terms, conditions for high levels of feeding and growth, reproduction, and low predation seldom coincide spatially (or temporally). Hence, sedentary populations typically contain fewer individuals and are less productive than migratory populations. It is no coincidence that commercial fisheries that rely on large biomasses of fish are prosecuted for the most part on migratory populations (Harden Jones, 1968). As with other long distance migrators, fish can be expected to have developed specialized migratory behaviors to facilitate exploitation of environments characterized by heterogeneity and structure, in the marine case in temperature, salinity, tidal, and current fields and attendant biological communities. These behaviors must influence the spatial patterns of migratory populations.

Questions on migratory behaviors (and energetics) cannot be addressed without data on swimming speeds through the water (not ground speeds). To calculate swimming speeds, both fish movements and ambient currents must be measured simultaneously. As stated by Harden Jones (1968) with respect to fish migrations, “one of the fundamental questions to be asked, and answered, is simply this: what are the movements of migrants relative to those of the water at the depth at which they are swimming? No critical data are available for any species on migration in the open sea.” Since that publication, technical advances in sonar and tagging technologies have led to a few reports of open-water swimming speeds (e.g. Arnold *et al.*, 1994), but still, as a consequence of the difficulty of making such observations, most reports of swimming speeds continue to be based on laboratory studies (e.g. Björnsson, 1993).

Historically, Atlantic cod spawned on the north-east Newfoundland shelf in late winter and spring then migrated shoreward across the shelf to the inshore summer feeding grounds, annually traversing distances

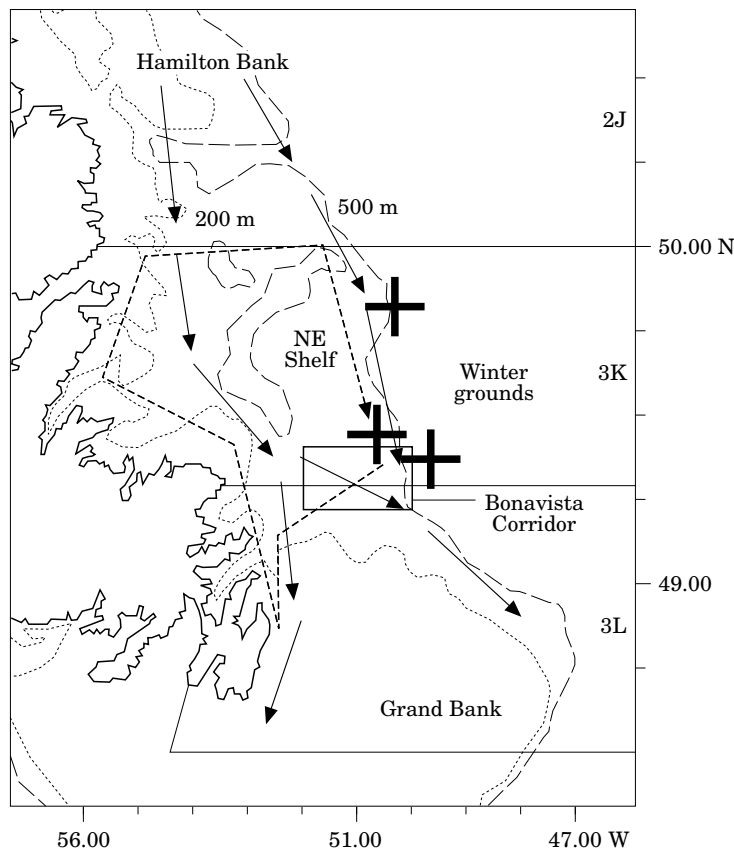


Figure 1. Map of north-east Newfoundland shelf and Hamilton Bank (NAFO Divisions 2J, 3K and 3L). Black arrows indicate dominant flows of Labrador current. Lighter line represents approximate outer migration routes, and crosses wintering grounds, for cod in 1990–1992. Box represents Bonavista migration corridor study area as in Figure 2.

of 500 km and perhaps much more (Templeman, 1966; Lear and Green, 1984) (Fig. 1). Cross-shelf migration routes in spring followed thermal “highways” along deeper basins and trenches wherein the warmer, deeper, north-west Atlantic waters in which cod overwintered and spawned, undercut the colder surface waters of the Labrador current (Rose, 1993). During summer, cod migrated northward along the coast, perhaps in conjunction with the movements of their chief prey, capelin (*Mallotus villosus*). In autumn, most cod migrated offshore back to their wintering areas. An unknown, but likely small proportion, remained inshore year-round (e.g. Wroblewski *et al.*, 1994). On the north-east shelf, cod feed little in winter and during spawning (Templeman, 1965) and are typically in poor condition by the start of the spring onshore migration.

Cod on the north-east Newfoundland shelf initially move southward after spawning (Templeman and Fleming, 1962; Templeman, 1979; Rose, 1993) with the dominant currents. However, once they turn shoreward, as they do within the Bonavista corridor, the dominant currents may flow offshore, against and across the

direction of the migration (Fig. 1). But flows in the deeper and warmer waters of the corridor at times reverse and flow shoreward (Narayanan *et al.*, 1991). This potential directional variability in the flows along the migration route led us to postulate hypotheses on cod migrations relative to these currents: (1) cod would passively drift during portions of the migration with some component of the flows; (2) cod would use an active form of movement (swimming with advancing currents and stemming opposing flows by staying nearer the bottom); and (3) cod would migrate against opposing flows. An alternative hypothesis was that cod would migrate without regard to currents but would move shoreward with increasing sea temperatures.

From 1990–1992, cod were tracked during their spring onshore migrations along the Bonavista corridor (Rose, 1993), in conjunction with oceanographic studies. In this paper, we use the cod tracking and oceanographic data to calculate daily ground and swimming speeds, distances travelled, and headings of cod along the route. We then test the transport hypotheses and discuss their

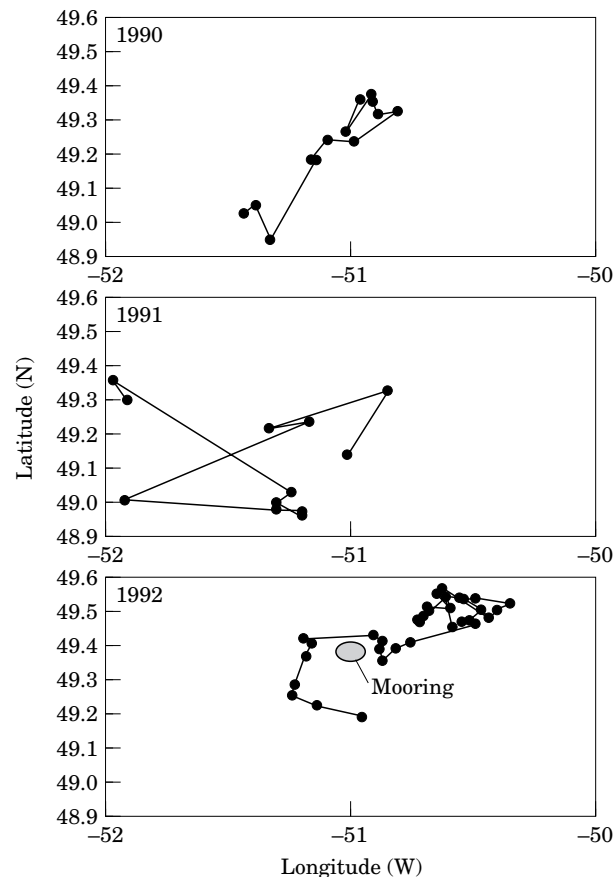


Figure 2. Bonavista migration corridor study area and daily migration tracks of cod from 6–18 June 1990, 14–23 June 1991, and 9 June–15 July 1992. Current meter mooring position in 1992 shown.

importance to the maintenance of population distributions and dynamics on the north-east Newfoundland shelf.

Methods

In 1990, 1991, and 1992, vessels equipped with scientific echo-sounders were employed to track large aggregations of migrating cod (dimensions in tens of km) across the north-east Newfoundland Shelf along the Bonavista cod migration “highway” (Rose, 1993). Echo-sounders were dual beam 38 kHz systems calibrated with standard reference spheres (tungsten-carbide 38 mm) prior to and after each tracking event (Biosonics, Inc., Seattle, WA, USA). In 1990 and 1992, single large shoals were tracked for 14 and 36 d, respectively, whereas in 1991 two shoals were tracked; the first broke up on contact with capelin (*Mallotus villosus*) shoals in the Bonavista saddle area; the second was tracked for only 3 d and is not reported here (Fig. 2). The transect strategy was to criss-cross the aggregation continuously, always attempting to cut the center and define the edges. Standard echo-integration

methods were used to calculate relative acoustic densities over a grid with horizontal and vertical dimensions of 1000 by 10 m (MacLennan and Simmonds, 1992). Species identification was based on echogram and individual echo characteristics (Rose and Leggett, 1988a; Rose, 1992) supported by mid-water and bottom trawling (an average of 2 sets d^{-1}). From backscatter or counts classified as cod, centroids were calculated as mean positions (latitude and longitude) weighted by cod density/numbers. An index of the total acoustic backscatter from cod measured daily (the sum of the densities integrated over the standard 1000 m sample grid) enabled a comparison of the abundance of fish tracked daily in 1992. A comparable index could not be calculated for each day in 1990 because acoustic data was collected only as target strengths on some days. Aggregation heights were calculated as the distance off the bottom that included 95% of the fish.

To examine the transport hypotheses, we use the tracking data on single shoals from 1990 and 1992 (the oceanographic data for 1991 was judged to be inadequate to assess thermal changes or water flows). In

Table 1. Summary of daily migration statistics for tracking and observational studies conducted on cod on the north-east Newfoundland shelf. Asterisks indicate values differ as assessed by Duncan's multiple range test ($p < 0.05$).

	1990	1991	1992
Tracking dates	6–18 June	14–23 June	9 July–15 July
Mean displacement (m)	9600	24 063*	6591
Maximum displacement (m)	28 710	59 019	19 017
Mean migration track (198°) (m)	3717	4913	1398*
Maximum migration track (198°) (m)	28 322	46 685	11 249
Mean ground speed (ms^{-1})	0.11	0.28*	0.08
Maximum ground speed (ms^{-1})	0.33	0.68	0.23
Mean swimming speed (ms^{-1})	—	—	0.10 (0.23 bl s^{-1})
Maximum swimming speed (ms^{-1})	—	—	0.28 (0.64 bl s^{-1})
Mean migration heading ($^\circ$)	198	199	198
Cross track deviation (%)	50*	130	160

1990, temperature profiles were taken daily at stations on the migratory route within the study area (Fig. 1). We used the daily rises and falls of the 2°C isotherm as diagnostic of shoreward and seaward cross-shelf currents (Narayanan *et al.*, 1991). In 1992, a grid of ten current meter moorings was placed along the route. Each mooring included an Anderraa current meter that measured temperature, salinity, and current flow each 15 min placed approximately 15 m off bottom. For our analyses, we used data from the station directly crossed by migrating cod (Fig. 2).

For analyses, current and cod movement vectors have been resolved around 18° and 108° (the axis of the Bonavista corridor and its cross component). This rotation was based on the mean heading of the cod during the three years of observation (198°). Note that shoreward directions are negative for both vector components (e.g. 198° directly opposes 18°). Swimming speeds were calculated by subtracting current from ground speed components. Note that our swimming speeds are applicable to the entire aggregation and are likely to underestimate the mean swimming speed of all individuals, because they are calculated as a straight line between daily centroids.

Results

Cod displacements averaged from $6.6\text{--}24\text{ km d}^{-1}$ from 1990–1992, and peaked at 59 km in a single day in 1991 (Table 1). Mean displacements did not differ between 1990 and 1992 but were higher in 1991 ($p < 0.05$). Migration rates over ground along the mean route (198°) averaged $1.4\text{--}4.9\text{ km d}^{-1}$, with a maximum of 47 km d^{-1} occurring in 1991 (Table 1). Mean migration rates did not differ between 1990 and 1991 but were lower in 1992 ($p < 0.05$). Mean daily ground speeds ranged from $0.08\text{--}0.28\text{ m s}^{-1}$ (1990 and 1992 not different but 1991 higher, $p < 0.05$) and peaked on a single day in 1991 (0.68 m s^{-1}). In all years movements occurred

sporadically rather than regularly (Fig. 2). Long-distance movements were rare.

Mean migration track headings were almost identical in 1990, 1991, and 1992 (198° ; Table 1). However, the cross-track deviations from the mean route heading (components resolved 90° to the highway) were much lower in 1990 than in 1991 and 1992 ($p < 0.05$; Table 1).

From 6–18 June 1990, the major cod movement occurred between 11–16 June, with notable stalling on 15 June and again on 17 and 18 June (Fig. 2). Greatest movements along the route corresponded with the greatest rises of fish off-bottom and with elevations of the 2°C isotherm (Fig. 3). Cod typically were concentrated in the bottom 25–50 m when less mobile but moved upwards in the water to 200 m off the bottom during migration (Fig. 4). These movements were superimposed on irregular but nonetheless apparent diel vertical movements of lesser magnitude that are not dealt with here. There was no trend in the total biomass assessed daily over the study period ($p > 0.05$). Somewhat larger cod were caught in the final third of the study than in the first two thirds ($p < 0.05$) (Table 2).

In 1991, cod were tracked for 9 d (Fig. 2). At the end of the tracking period the aggregation had broken up as fish separated from the main aggregation to follow capelin towards the north-west. Cod travelling north-west were tracked for 2 d (Fig. 2).

In 1992, cod were tracked for 36 d (9 June–15 July) (Fig. 2). Tracking began with the location of a large spawning aggregation at a depth of 350 m near the offshore margins of the highway (see Rose, 1993). Cod were distributed further off-bottom when actively migrating shoreward than during spawning and more sedentary periods (Fig. 5). Typically, cod ranged up to 150 m off-bottom during migration with highest densities in the mid-ranges of their distribution (Fig. 6). When more sedentary, most fish were located in the bottom 50 m with highest densities in the bottom 25 m (Fig. 6). During the migratory period, movements along

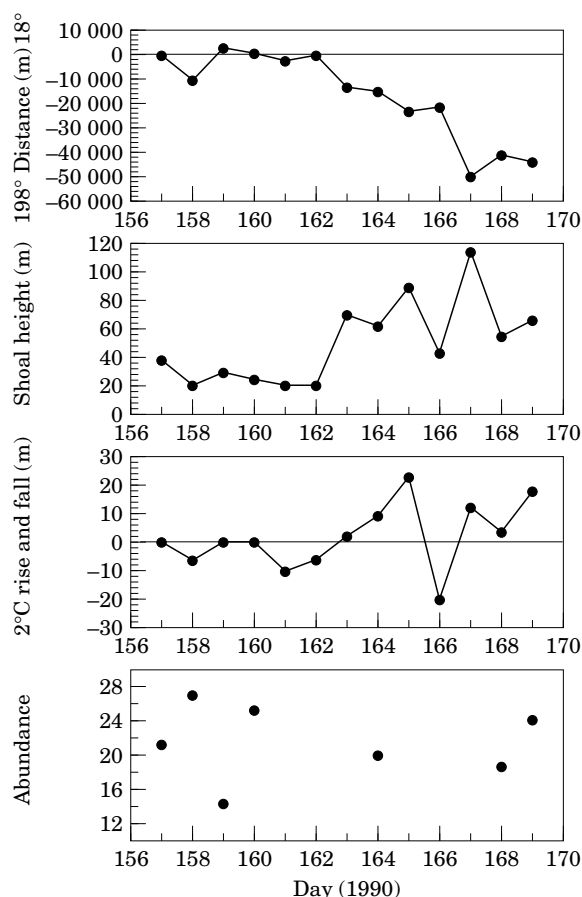


Figure 3. For 1990, cumulative component of cod migration vector along mean route (198°) (top); depth from bottom that encompasses 95% of cod (middle); rise and fall of 2°C isotherm, mean of 2 stations along the route (middle bottom), and an index of total biomass observed daily (note that the biomass series is incomplete because density estimates were not made daily).

the route were greatest from days 178–186 and 191–194 and coincided with increasing temperatures at 325 m (Fig. 5). The stalling that occurred from days 186–191 coincided with cooler waters at 325 m. There was no trend in the index of total biomass assessed daily over the study period ($p > 0.05$) (Fig. 5). On average, larger fish were caught in the initial period, but this difference was less than 1 cm ($p > 0.05$) (Table 2).

Daily swimming speeds were on average slightly greater than ground speeds (paired t -test, $p < 0.05$), averaged 10 m s^{-1} , and ranged up to 0.28 m s^{-1} . During June, when spawning occurred, cod movements did not appear to be directed shoreward. However, beginning on 2 July, cod movements were shoreward on 10 out of 13 d (Figs 2, 5).

The transport hypotheses were examined according to a model comparing swimming (speed relative to water)

and ground speeds (Fig. 7). Passive transport would be indicated by a zero slope. A slope of 1 would indicate that swimming dominated flows. Active transport would be indicated by a non-linear relationship between swimming and ground speeds such that forward motions (flows exploited) would have $\text{groundspeeds} > \text{waterspeeds}$ whereas backward motions (flows resisted) would have $\text{waterspeeds} > \text{groundspeeds}$. Cod swimming and ground speed components across the mean migration route (108°) were strongly correlated with a slope not different from unity ($r = 0.94$, $\text{s.e.} = 0.05$, $p < 0.05$) (Fig. 8a). The fit between swimming and ground speeds along the route (198°) was less clear. A linear model fit the data rather poorly ($r = 0.24$, $p < 0.05$), but the overall slope did not differ from unity (slope = 0.85, $\text{s.e.} = 0.15$, $p > 0.05$) (Fig. 8b). However, a non-linear fit indicated a stronger correlation ($r = 0.30$) with a shape consistent with the model for active transport (Fig. 8a). As further evidence of active movements, the migration consisted of stops and starts and, on the two days of greatest movement along the “highway”, cod groundspeeds averaged 0.13 m s^{-1} while swimming speeds averaged only 0.08 m s^{-1} . However, on other days, cod apparently swam only very slowly or not at all with shoreward currents, or even short distances backwards to the north-east (18°).

Discussion

Our data indicate that migration rates, as indicated by ground speeds, are typically quite slow but highly variable as cod cross the north-east Newfoundland shelf. Mean ground speeds were only $0.08\text{--}0.28 \text{ m s}^{-1}$ ($0.2\text{--}0.6 \text{ bl s}^{-1}$); maximums for the three years ranged from $0.23\text{--}0.68 \text{ m s}^{-1}$ ($0.5\text{--}1.5 \text{ bl s}^{-1}$). The maximum distance covered over ground in a single day was 59 km (1991), but distances of approximately 20 km were travelled daily in all years. Danke (1967) and Postolaky (1966) reported that cod on the Labrador shelf migrated a maximum of $36\text{--}40 \text{ km d}^{-1}$ southward after spawning, based on tagging studies (presumably with the flows). It is noteworthy that the largest displacements were observed in 1991, the only year cod encountered and fed on their chief prey, capelin, in the offshore regions of the migration highway (see Rose, 1993). The lesser displacements recorded in 1990 and 1992 may reflect the differing feeding patterns and the poorer condition of the fish in those years. Laboratory experiments that have shown a dome-shaped relationship between swimming speed and food intake suggest that, under conditions of abundant food, the potential pay-offs make energy-saving strategies (Ware, 1975) less necessary (Bjornsson, 1993). However, the lack of flow data made it impossible to assess swimming speeds in 1991.

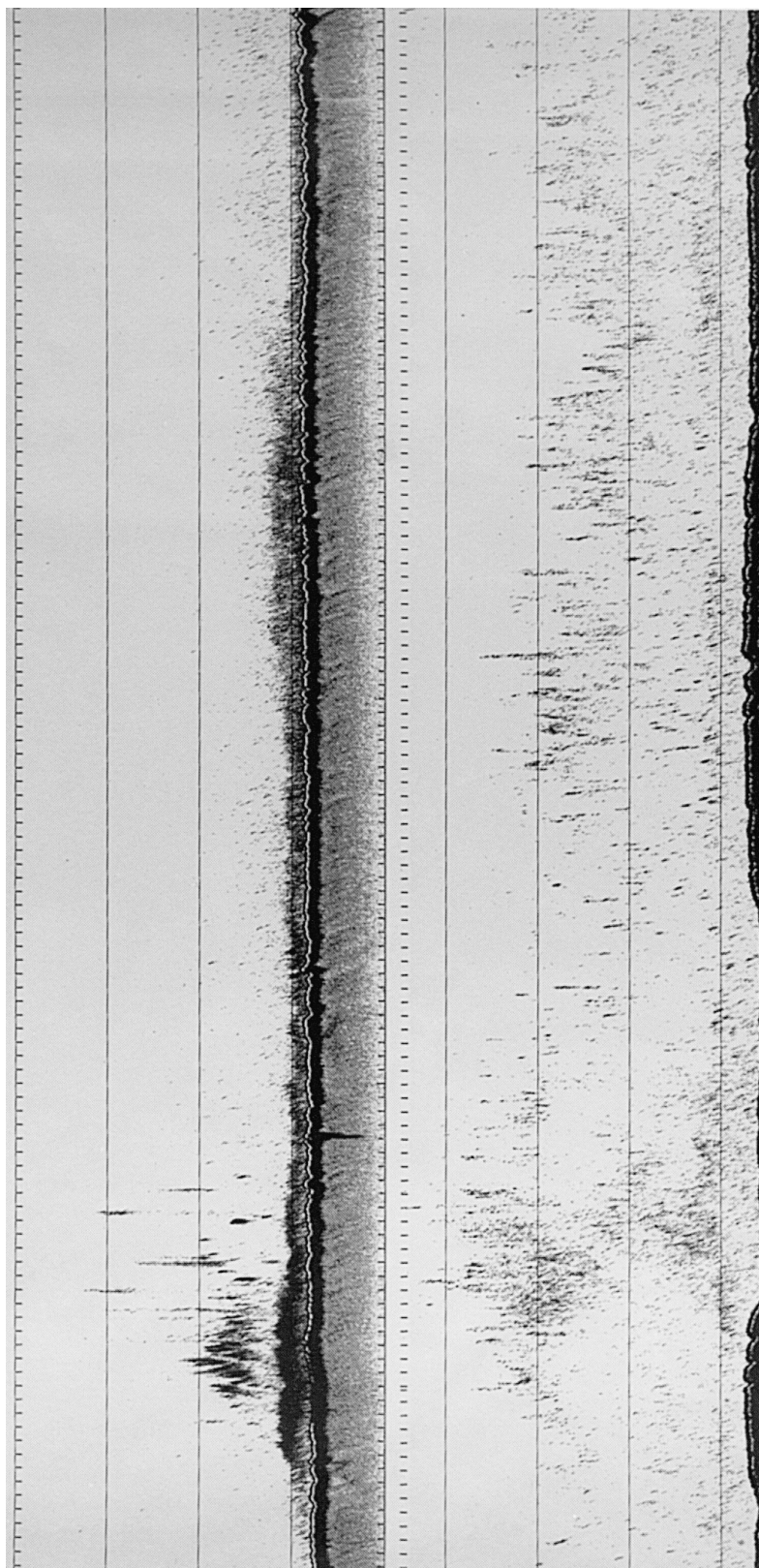


Figure 4. Echograms from 1990 showing cod near bottom on 10 June, a day of little movement (top panel) and up in water on 14 June, a day of strong movement (bottom panel). Echograms have common scales: horizontal distance 10 n miles, total depths 350 m, each vertical grid 50 m (only bottom waters shown).

Table 2. Cod length statistics for the first (1), middle (2), and last (3) thirds of the 1990 and 1992 study periods from fishing sets; nsets is number of fishing sets. Lengths between years differ ($p < 0.05$). Asterisks indicate within years values differ as assessed by Duncan's multiple range test ($p < 0.05$).

	Time	Mean (cm)	s.d.	n	nsets
1990	1	50.4	9.6	2167	10
	2	51.9	9.2	764	4
	3	55.2*	9.6	202	2
1992	1	45.8*	7.2	1109	5
	2	45.0	7.7	2457	16
	3	44.7	7.0	4193	33

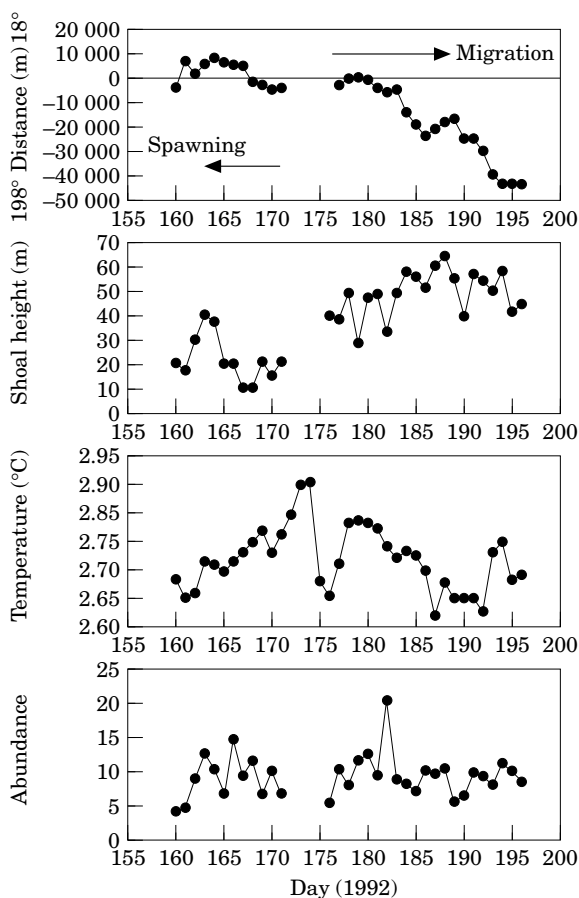


Figure 5. For 1992, cumulative component of cod migration vector along mean route (198°) (top); depth from bottom that encompasses 95% of cod (middle); temperature at mooring on migration route 15 m off-bottom, and an index of total biomass observed each day.

Our data also show that, at least in 1992, cod swam relatively slowly most of the time. Daily swimming speeds averaged 0.10 m s^{-1} (0.23 bl s^{-1}) and peaked at 0.28 m s^{-1} (0.62 bl s^{-1}). Note that any individual fish may have travelled at a greater speed. As expected, these

swimming speeds are well below maximum swimming speeds demonstrated in laboratory studies. For example, Blaxter and Dickson (1959) reported that cod of a size equivalent to those in our study (40–60 cm) had maximum swimming speeds of $1\text{--}1.5 \text{ m s}^{-1}$ over short distances (67 m). Beamish (1966) reported that cod could sustain $2\text{--}3 \text{ bl s}^{-1}$ ($1\text{--}1.5 \text{ m s}^{-1}$) for more than 4 h. It is noteworthy that if cod swam as Beamish (1966) shows for 4 h in a day, then stopped, they would swim a maximum speed of 0.21 m s^{-1} and cover a distance of approximately 18 km daily. These predictions are very close to our observed maximum values (0.28 m s^{-1} and 22 km). Other studies have reported sustained speeds of $0.4\text{--}0.8 \text{ m s}^{-1}$ (Wardle, 1977; Tytler, 1978), and 0.5 m s^{-1} for 40–50 cm cod (Bjornsson, 1993). Jones (1978) reported average swimming speeds of cod to be 0.21 bl s^{-1} at 6°C in a laboratory study. Only one other detailed field study is known; average swimming speeds of cod during tidal stream transport in the North Sea have been reported to be $0.3\text{--}0.9 \text{ bl s}^{-1}$ (Arnold *et al.*, 1994). These sustained average swimming speeds are similar in magnitude to those in our study, but, as would be expected, are somewhat higher as they are based on movements of single fish.

We conclude that cod foraging movements are sporadic and that searches for prey in general occur at slow speeds. It is noteworthy that submarine searching theory suggests that a predator searching for a mobile prey should move relatively slowly to optimize search efficiency. In a laboratory study, Bjornsson (1993) reported that cod swam continuously but at slow speeds when prey availability was low (as it was during 1990 and 1992). Once inshore and amongst the capelin, cod may reduce their movements even further and let the prey come to them (Horne, 1994). The relationships between swimming speeds, foraging activities, and prey distribution patterns will be examined more fully in additional papers.

Cod tended to move shoreward along the migration “highway” (Rose, 1993) with advancing warmer waters in both 1990 and 1992. This finding supports the contention that the migratory route is at least partially determined by thermal conditions (Rose, 1993). Migration patterns of cod in the Barents Sea have also been attributed to thermal conditions so that the successes of spatially diverse fisheries could be accounted for by sea temperature variations (Konstantinov, 1965). Relationships between water masses (temperature as the key factor or proxy for others) and cod distribution have long been known by fishermen and scientists (Harvey, 1894; Jeffers, 1931; Thompson, 1943; Lee, 1952; Trout, 1957; Jean, 1964; Beverton and Lee, 1965; Templeman, 1966, 1979; Harden Jones, 1968; Nakken and Raknes, 1987; Rose and Leggett, 1988b; Rose *et al.*, 1994).

Did cod utilize active or passive transport to migrate? During migration, cod moved upwards into the water,

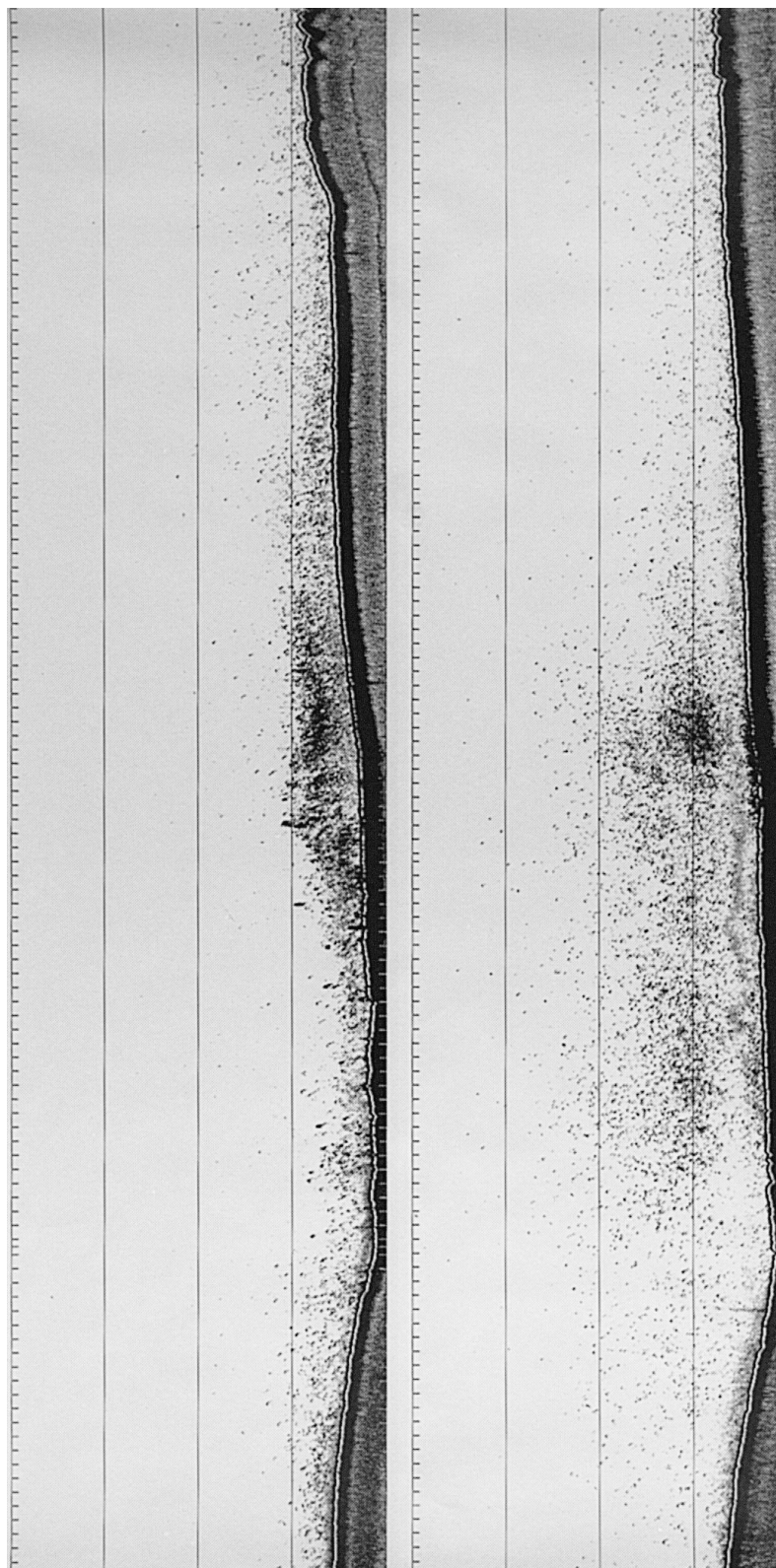


Figure 6. Echograms from 1992 showing cod near bottom on 8 July, a day of little movement (top panel) and up in water on 9 July, a day of strong movement (bottom panel). Echograms have common scales: horizontal distance 10 n miles, total depths 350 m, each vertical grid 50 m (only bottom waters shown).

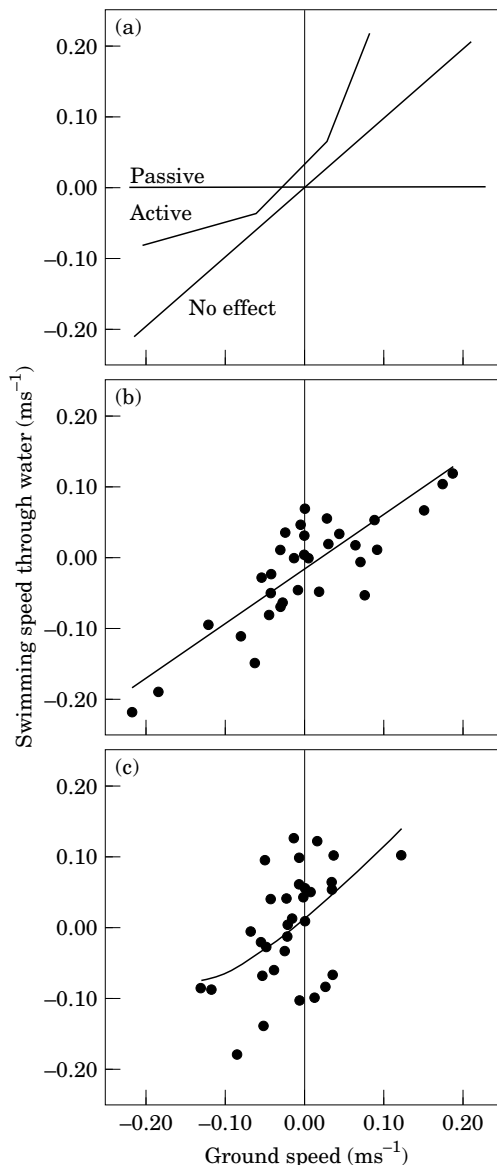


Figure 7. (a) Theoretical relationships between swimming and ground speeds indicating passive motion, no effect of currents on movement, and active transport; (b) observed speeds along cross route direction (108°) and best fit linear model ($r=0.9$, $p<0.05$); (c) observed speeds along mean migration route (198°) and best fit quadratic model ($r=0.3$, $p<0.05$).

as expected. Perhaps upward movements increased buoyancy (Arnold and Greer Walker, 1992) and reduced energy expenditures attributable to swimming. At times, cod swam with advancing flows, thereby increasing ground speeds and distances travelled to well beyond those attributable to drift or swimming alone. Of note is that the major cod movements shoreward coincided with shoreward or slack currents. On other days cod appeared to drift with currents, but only along the route,

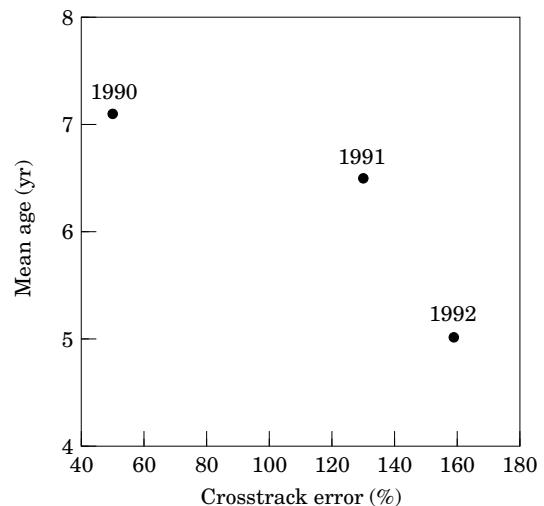


Figure 8. Migration cross-track error (108° component as percentage of 18° component of ground speed vector) relative to mean age of fish migrating across north-east Newfoundland shelf along Bonavista "highway" for the years 1990–1992.

with very low swimming speeds. In contrast, no passive movements were evident in the directions across the route. This is especially important because cross-track currents are the dominant flows (Fig. 1). Also of note is that cod did not retreat along the highway to any great extent during migration when flows were seaward and tended to stay near the bottom in the majority of cases. Hence, the active transport hypothesis is supported. Passive transport was observed along the route on several days (swimming speeds near zero). There was little evidence of cod attempting to gain ground while swimming against currents. However, there are exceptions to these generalizations, and there were days when active transport shoreward did not appear to hold – as if on these occasions cod were responding to other factors. In a similar way, cod in the North Sea did not always appear to use tidal stream transport (Arnold *et al.*, 1994). We strongly suspect that foraging behavior had a major influence on cod movement patterns (e.g. Beverton and Lee, 1965; Rose and Leggett, 1989, 1990).

The strength of our findings on swimming speeds and migration directions depends on the accuracy of the estimated daily centroids as representative of the positions of single bodies of fish. In both 1990 and 1992 the migrating cod formed a discrete aggregation during the periods of observation (e.g. Figs 4, 6). In both years, the echo-sounding vessel was in almost continuous contact with the aggregation, broken only for periods of hours when surrounding regions were sounded, except for the ship change in 1992. Moreover, our data on total acoustic abundance suggests that the aggregations did not fragment during our observations in 1990 and 1992 (the data used to calculate swimming speeds). In

contrast, we observed fragmentation in 1991, after cod contacted large capelin shoals, and we have not used these data to calculate movement. The average lengths of cod caught did change somewhat over the periods of study. Most notable is the much smaller size in 1992 than in 1990, but there was also within-year variation. However, much of this variation is likely due to the fewer sets conducted in the periods that differ. Cod are not randomly distributed within the shoal with respect to size (Rose, 1993), hence a lower number of sets could result in bias in fish size data. In particular, the larger size of fish caught in the final part of the 1990 tracking are likely to have resulted from attempts to keep to the front of the shoal as it moved relatively quickly. The front running fish are larger than the rearguard (Rose, 1993). In contrast, larger fish on average were taken at the beginning of the 1992 study. This result almost certainly occurred as a consequence of the spawning behavior in 1992 at the beginning of the study and the concentration of sampling on older fish then, and a more systematic sampling of the entire aggregation during the latter part of the study than in 1990. None of these factors are believed to have significant impacts on centroid accuracy.

Some energetic advantage may be achieved through active transport. Cod on the north-east shelf are in poor condition following a winter of few feeding opportunities and spawning (Rose, unpubl.). Even though the energetic savings may be small in absolute terms (e.g. Tytler, 1969; Horne, 1994), savings could still be relatively important to fish with low energy reserves (Bjornsson, 1993). Consider that, on the three days when cod moved backward during the migration at $0.01\text{--}0.04\text{ m s}^{-1}$, they remained near the bottom with moderate forward swimming speeds ($0.07\text{--}0.10\text{ m s}^{-1}$). This result suggests that during strong seaward flows cod may have attempted to hold position but did not attempt to gain ground by out-swimming the currents. Individual cod have been shown to exhibit similar behavior (Arnold *et al.*, 1994). Active down-current swimming, which may be needed to achieve energetic savings (Metcalfe *et al.*, 1990), was also observed in the present study.

Finally, our data demonstrate that cod migrations can be conducted with great inter-annual precision despite apparently low day-to-day accuracy. Despite frequent meanders, the mean headings taken by cod varied by less than one degree over the same ground in three years of study! Our data do not enable us to address the question of how this direction was maintained. But a few comments are in order. The general confines of the migration appear to be set by the thermal limits and bathymetry of the migration “highways” (Rose, 1993). The thermal properties of the “highways” are relatively stable and spatially persistent from year to year, and perhaps the mean heading simply reflects the mean axis of the

persistent thermal and bathymetric route used by cod as they follow the cross-shelf warm water incursions of the “highways” across the shelf. Dominant current flows fluctuate widely, but for the most part occur across the route. Thus, current shears are unlikely to provide reliable cross-shelf directional information. Several other possibilities exist as to shoreward clues (see Arnold *et al.*, 1994). No matter what the clues are, if they are persistent, then the routes could be learned. Younger fish have been observed to conduct “dummy runs” accompanying older fish to spawning areas and to follow larger fish during migrations (Harden Jones, 1968; Rose, 1993). Under this paradigm, older fish would follow known landmarks (seamarks) experienced and learned in previous years (e.g. Baker, 1978). Younger fish would follow. It is noteworthy that the cross-track error, which can be considered an index of the directivity of the migration, was associated with the age structure of the population (the younger the population the greater error, Fig. 8). Learning of migration routes has been demonstrated in tropical reef fishes (e.g. Ogden and Quinn, 1984). If migration routes are learned, even in part, then the dramatic declines in older northern cod in the early 1990s might be expected to lead to equally dramatic changes in migration patterns.

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